

## 7.0 INTRODUCTION TO POPULATION ASSESSMENT

### 7.1 Viable populations

There has been much interest in recent years in maintaining viable populations of various species. Many of the efforts stem from the requirements of the Marine Mammal Protection Act of 1972 and the Endangered Species Act of 1973. Due to the complexities of natural systems, legislative mandates often cannot readily be translated into programs that can actually be implemented in a field setting. Thus an early question was "what is a viable population?" One attempt at an answer led to definition of a "Minimum Viable Population" (MVP) as the population size that had a 95% probability of surviving for 100 years. Stochastic population models were implemented on a computer and starting population size varied to find an initial population size that resulted in about 5% of the simulated population going extinct in 100 years. A major problem with such models is that the outcomes depend very much on the set of parameter estimates used in the model. If the parameters are such that the average population trend is a decrease, then higher initial population levels are required to meet the criterion than if the expected trend is upwards. Interpreting the available field data provides another pitfall -- three such stochastic models have been published that consider the Yellowstone grizzly bear population, all with shortcomings of interpretation.

When the difficulties in the Minimum Viable Population approach began to become apparent, appraisals using less specific and broader methodology were developed and described as Population Viability Analysis (PVA). Various kinds of models continued to be emphasized for the analysis of populations of endangered species (Soule 1987). These broader appraisals of Population Viability Analysis include the important feature of the possible loss of genetic variability, but there is as yet considerable controversy about the minimum population size required to preserve sufficient genetic variability to maintain the species (Boyce 1992). It does seem to be generally accepted that an occasional exchange between isolated subpopulations is sufficient to maintain genetic diversity, so that the genetic issue may be of major importance when only one small remnant of a species exists.

A crucial uncertainty in modeling any natural population is the poorly understood role of density-dependence. Consider a population containing 50 females in which births and deaths are balanced so that the expected trend is to remain constant ( $\lambda = 1.00$ ). If a stochastic model with no density-dependence is run 1,000 times for 100 years each run, the outcomes may be as in Fig. 7.1, in which 16 "populations" were extirpated, thus meeting the MVP criterion of "viable". If density-dependence is introduced, a much smaller population (10 females) can be observed for 100 years (1,000 runs) with no extirpations (Figure 7.2).

Until much more is known about the mechanisms controlling trends in small populations, the most prudent approach to maintaining viable populations is to concentrate on "population analysis", that is, to determine survival and reproductive rates in an effort to determine whether the population can be expected to increase or decrease in the immediate future. If a decrease seems likely, then management actions need to be directed towards changing the rate most likely to be responsible. First-year or adult survival appear to be responsible in the available examples. The same general

principle appears to apply in those cases where the goals are to control an over-numerous population or to secure a maximum sustainable yield from an exploited population.

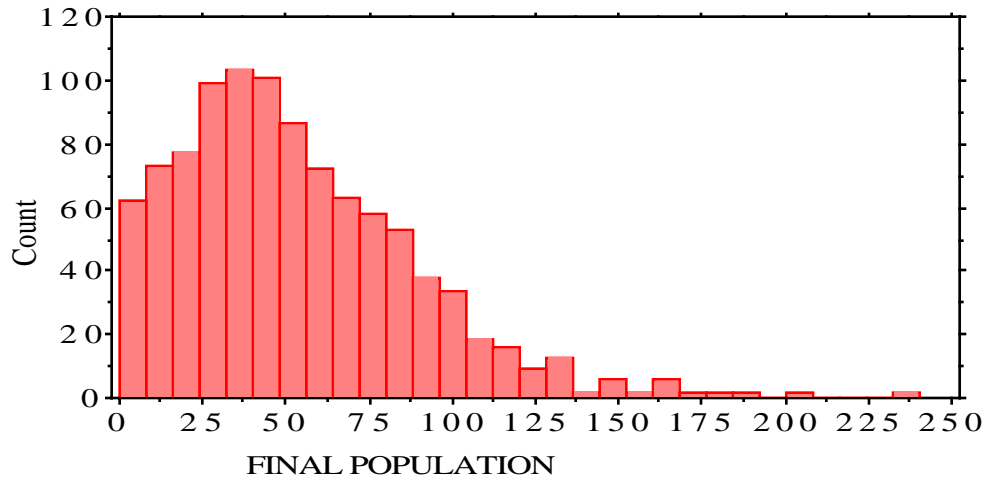


Fig. 7.1. Outcomes of 1,000 simulation runs of a population starting with 50 females with parameters selected to give  $\lambda = 1.00$ , and no density dependence.

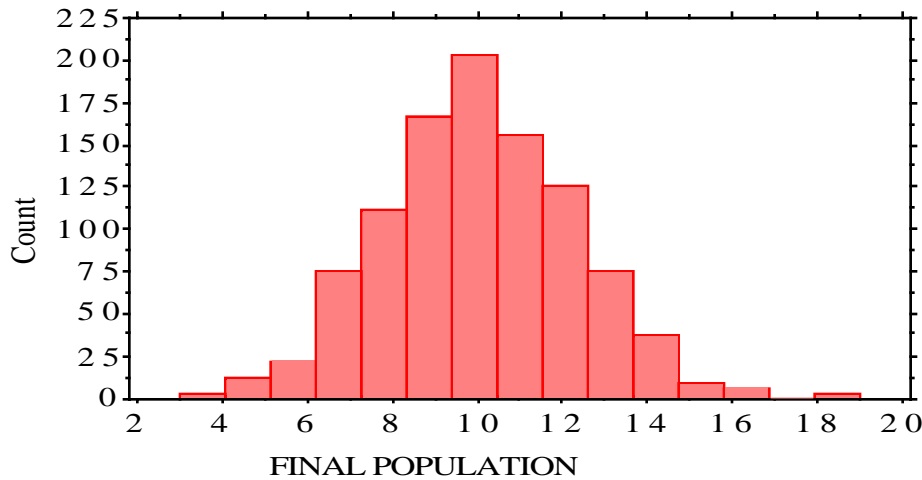


Fig. 7.2. Outcomes of 1,000 simulation runs of 100 years for an initial population of 10 females with a density-dependence function acting on first-year survival and "carrying-capacity" (K) set at 10 females.

Many studies may require 10 years or more to obtain enough data to determine the key issues, and to begin to develop effective approaches to solutions. Often the initial assessments of the perceived problem turn out to be in error, and it may take a long time to correct these initial perceptions in the face of public pressure to "do something". While the "environmental movement" has created a climate in which actions to maintain endangered or threatened species have become possible, the many private organizations dedicated to fostering such actions may hamper progress in particular cases. This usually results from the need to demonstrate their active participation in order to maintain a flow of funds from the public. Litigation engenders

publicity and thus funding, but may also seriously limit the ability of a responsible agency to obtain required data.

## 7.2 Methods for population analysis

Administrators and the general public always ask "How many are there?" when faced with some issue concerning a population. This seems to be a wholly reasonable question, and is one that often has to be answered in one way or another. If sizable removals are made for exploitation or control purposes, an estimate of absolute numbers may be essential, in order to assess the likely impact of the removals. Endangered species are often present in low densities, and may thus be very difficult to census. Consequently, an investigator may expend much of the available resources in an attempt to obtain a population estimate, only to discover that the precision of the estimate is not adequate for the major goal of any study of an endangered species. This almost always has to be one of determining trend of the population. If, as usually seems to be the case, a very large effort has to be expended to get a census estimate of relatively low precision, then repeating the census in another year very likely will not supply a useful measure of trend.

There are basically two alternatives. One is to opt for some measure of trend based on an index of abundance that may be much less expensive to obtain than an estimate of absolute abundance. The other is to obtain reproductive and survival data on which to base an estimate of likely trend. This has a distinct advantage for studies of endangered species, inasmuch as such studies usually also need to try to determine why the species is "in trouble" and what might be done to insure a positive rate of increase. If one relies only on trend data, it likely will take a sizable number of years to establish a trend, and the mere observation of trend will not provide any information on reasons for the change. It is true that the basic cause for a declining trend may be obvious, i.e., loss of suitable habitat. Nonetheless, it may be essential to know how this cause affects rate of change in the population, and this requires knowledge of reproductive and survival rates. If positive steps to reverse a decline can be taken, then the impact of such steps will most likely first be evident in reproductive and survival rates.

Virtually all field data on large populations is inadequate in scope for "textbook" analyses of present status and likely future trends of the population. Each data set has unique features, often in consequence of the unique nature of the particular species, but also because of the difficulties and costs of data collection. A variety of approaches is thus required, including various kinds of approximations and indirect methods of estimating essential parameters of the population. The present study is concerned with development and evaluation of such approaches to actual field data on a diverse array of species.

Most field studies of large populations seek to predict the future trend of a population by assessing data collected over time. In some instances either research goals or a legislative mandate (see, for example, Eberhardt 1977a) may direct attention mainly to the past, often with a goal of evaluating present status of the population or predicting the likely impact of some alteration of the landscape or its uses. A universal need in such studies is to evaluate likely accuracy and precision of the outcome.

Because the methods used in practice all require assumptions that are very difficult to support under field conditions, the only satisfactory demonstration of accuracy may be independent estimates of the same quantity, usually rate of change of the population. This can be achieved by comparing estimates based on trend data (e.g., a log-linear regression of a population index) with those derived from reproductive and survival data. Most studies fall short of this goal through lack of estimates of some essential rate. Another need is thus to indicate something of the minimal requirements for assessing accuracy of a population study.

Uncertainty about fulfillment of assumptions has similar effects on precision for any given kind of estimate (e.g., of population size). Since an overall assessment will require a number of individual estimates, appraising precision of the end-product (e.g., a rate of increase) is also very difficult, and rarely attempted. The problem needs to be faced, however, because improving population analyses will likely depend on combining inferred parameter estimates (e.g., those derived from, say, age and sex ratio data) with direct measurements (obtained, for example, through radiotelemetry). Combining two such sources will usually require weighting by measures of precision. The non-parametric methods, such as bootstrapping and jackknifing, provide the necessary flexibility.

The basic ingredients for an assessment are measures of population size and estimates of reproductive and survival rates. These may be obtained in a variety of ways, and can be used in an analysis based on either a direct projection of population size or by estimating a rate of change from survival and reproductive rates alone. The major difference between the two is that projections require estimates of population size. We are thus concerned here with three sources of data and two methods of utilizing that data (Fig.7.3). A brief listing of the individual sources and methods given in Fig. 7.3 follows.

*Population estimation* can be approached by making direct estimates of actual abundance or through indices of abundance. There is a very large literature on methods for estimating animal abundance (Seber's 1982 book is still the major reference) and much theoretical and practical work continues to be published on these methods.

*Survival estimates* are usually obtained either indirectly through analysis of age structure data or directly through evaluation of data from tags and marks. Use of age structure data alone requires the very restrictive assumptions of constant population size and constant recruitment to the population in the years in which the age structure was developed, along with constant survival. If tags are used, then the assumption of constant recruitment is not needed in estimating survival from tag recoveries. A major advance has been use of radiotransmitters as tags, reducing uncertainties and variability associated with tag recoveries.

*Reproductive rate* data are usually more readily obtained than information on population size and survival. Often sizable numbers of individuals can be examined for pregnancy and age-specific rates derived directly. However, some species (e.g., bears and whales) do not reproduce annually, so that it may be necessary to use a composite measure of reproductive rate, based on sex ratios at birth, litter sizes, breeding intervals, and so on.

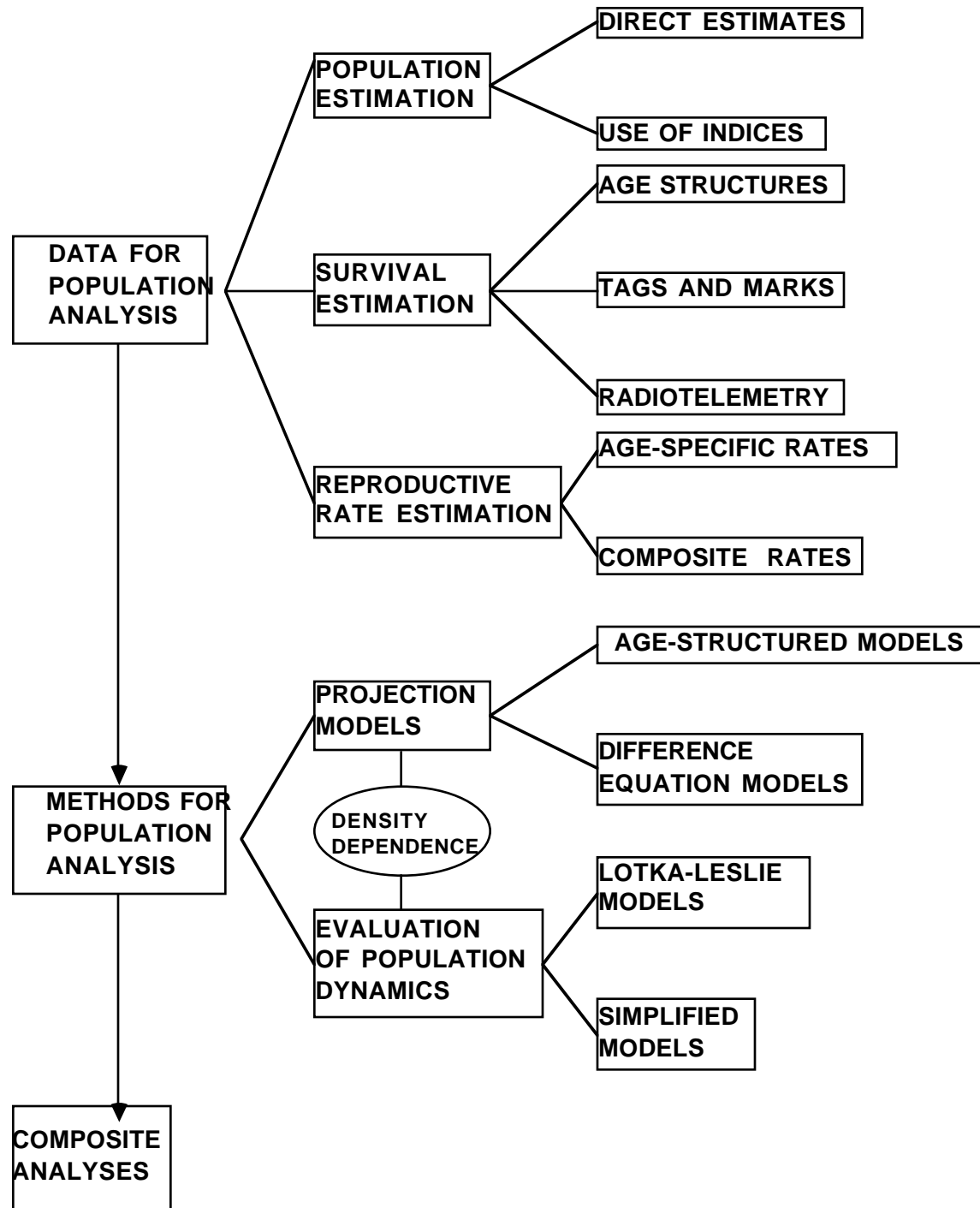


Figure 7.3 An outline of techniques useful in analysis of large vertebrate populations.

Methods for population assessment using the data outlined above can be considered in two classes. *Projection models* require an estimate of population

size and apply birth and death rates to project the population from one year to the next. The simplest such models that incorporate provisions for removal of known numbers of individuals are:

$$N_{t+1} = R(N_t - K_t) \quad (7.1)$$

$$N_{t+1} = RN_t - K_t \quad (7.2)$$

where  $K_t$  denotes removals at time  $t$  and  $R$  represents a rate of increase. The two equations differ in terms of whether the removal takes place just before or just after reproduction occurs. When age-specific birth and death rates are known, the equations may be written as *matrix models*, with  $R = \mathbf{M}$ , the Leslie matrix. When age-specific rates are not available, the equations may be expressed as simple *difference equation models*, with  $R = \lambda$ , a constant annual rate of increase.

One of the major difficulties in actual applications of projection models is the present uncertain state of knowledge about population regulation. If the prospect of *density dependence* is to be incorporated in the model, then some sort of functional form has to be assumed, operating directly on  $R$  for difference equation models and one or more of the elements of the Leslie matrix for age-structured data.

In the absence of population estimates, a direct *evaluation of population dynamics* may be conducted on the basis of age-specific reproductive and survival rates. The classical approach is that of A.J. Lotka, who first demonstrated that constant age-specific birth and death rates result ultimately in both exponential growth (or decline) and a constant relative age structure (the stable age distribution). Lotka's basic equation is equivalent to the characteristic equation of the Leslie matrix, so the models are here described as *Lotka-Leslie models*. In practical applications, there usually is not enough data to use more than a few reproductive and survival rates, so Figure 7.3 includes a class of simplified models based on these rates.

### 7.3 Population estimation

Although there is a large array of methods for estimating population densities, relatively few methods are actually used on large vertebrates. The principal techniques used in the field are transect methods and those based on harvest data (largely "catch-effort" methods). For the most part, the use of a limited set of methods is a consequence of the very large areas involved and the high costs of marking animals on such areas. The catch-effort methods have mainly been applied to marine mammals, usually give highly variable results, and suffer from several other difficulties (cf. Eberhardt, Chapman and Gilbert 1979). Transect methods are largely used from aircraft or ships and thus are frequently subject to uncertainty as to whether the assumptions required for density estimation are met (Eberhardt, Chapman and Gilbert 1979; Burnham, Anderson, and Laake 1980). As noted above, the major reference for estimating both population size and survival rates is the book by Seber (1982). A monograph by Pollock et al. (1990) provides some further discussion of underlying models and access to a computer program suitable for estimating parameters of these models. Program MARK maintained at Colorado State

University may be on of the most up-to-date of the many programs now available.

In many applications, it is likely that the data on population abundance have to be considered as an index, rather than as an estimate of absolute numbers. There are two difficulties. One is just that very little quantitative work has been done on indices. A more serious problem is that many field applications concern populations subject to harvesting or other removals. Since removals are expressed in absolute terms, it is necessary to also express population size in absolute terms, or to make the very restrictive assumption that removals are directly proportional to abundance. Because the projection models require estimates of absolute abundance, indices may be most useful to check calculation of a rate of change from the Lotka-Leslie models in those cases where the population is not subject to substantial removals.

Optimal use of index data for population analysis requires some sort of calibration to convert the index to an estimate of absolute abundance. Often a method that provides direct estimates is available, but is too expensive or time-consuming for application over the entire area of concern. The appropriate means for calibration may then be the statistical technique known as double sampling, in which small samples obtained through an expensive but accurate technique are used to make ratio or regression corrections to large samples obtained by a relatively inexpensive technique (the index). Unfortunately, the available statistical basis for the method depends on approximations, so that the usual recommendations for sample sizes (Cochran 1977) are larger than can be managed for many animal population studies. Some simulations indicate that smaller samples can be used, and various devices may be used to try to reduce the effort required for calibration (Eberhardt and Simmons 1987).

The principal alternative to calibrating an index may be large scale marking. For the most part, costs are too high to make capture-recapture uses of tagging and marking feasible for large populations inhabiting sizable areas, so that the technique has mainly been used to estimate survival. The high, stable survival rates necessarily exhibited by at least the adult female age classes of many species of large vertebrates suggest the possibility of periodic population estimates based on tagging or marking over a number of years, so that enough marks are built up in the population to yield reasonably precise estimates in a recapture series. DeMaster et al. (1980) reported one such attempt for polar bears, but assumed a constant, known survival rate for estimation purposes. Unfortunately, satisfactory direct estimates of survivorship are very difficult to obtain for this species (and most others). Consequently, it seems likely that progress along these lines will call for the imposition of appropriate restrictions on the Jolly-Seber method (see, for example, Brownie, Hines, and Nichols 1986).

#### 7.4 Survival estimation

Survival estimates are likely to be the most important ingredient in population analysis, yet are often the least satisfactory estimate obtained in actual practice. Their importance is due to the magnitude of the effect of a small difference in adult female survivorship on rate of change of the population (cf. Eberhardt and Siniff 1977). A few percentage points one way or another spell the difference between a comfortably increasing population and one threatened with extirpation. Subadult survival rates have markedly less

effect on rate of change, and may thus be the major factor in population regulation, while adult female survivorship quite possibly provides the last mechanism to come into play in a sequence of events under natural conditions (Eberhardt 1977b).

Poor quality or outright absence of survival estimates in many studies no doubt reflects the high cost of obtaining useful estimates. The least expensive route is via age structure data. If survivorship in adult age classes is constant from year to year, and the same number of individuals are recruited to adult status each year, then the ratio of numbers in successive age classes will ultimately reflect the common survival rate. Averaging over a number of age classes in a sample is necessary to reduce variability in the estimate, and Chapman and Robson (1960) described an efficient estimator for that purpose. Other methods can be very much less efficient (see Eberhardt 1972 for examples).

Unfortunately, the assumptions required for use of survival estimates from age data are so restrictive that they are unlikely to be met in practice, and should be tested whenever the method is used. A null hypothesis of constant annual survival rates plus constant recruitment implies that age structures in successive years should be homogeneous, so that chi-square might be used to test the hypothesis and thus the assumptions. However, such homogeneity is not a sufficient condition to justify estimating survival from age structure data since homogeneity of successive age structures is implied by the stable age distribution (Keyfitz 1968). Such a distribution results from populations changing at a constant rate. Consequently, adequate justification for using survival estimates from age structure data also requires a demonstration that population size has remained constant.

In many instances, a population may tend to increase (or decrease) at a relatively constant rate (examples are given by Eberhardt 1987). The Chapman-Robson method may then still be used, but now under the assumption of constant survival and of recruitments changing at a constant rate. The parameter estimated then becomes  $s/\lambda$ , where  $\lambda$  denotes the "finite population multiplier", i.e.,  $\lambda = e^r$  or  $\lambda = 1+r$  depending on whether continuous or discrete rates of population change are assumed.

The alternative to using age structure data is to mark or tag individuals, and estimate survival rates on the basis of rates of recovery of these individuals in subsequent years. This disposes of the assumption of constant recruitment, by virtue of the fact that the number of marked individuals is now known. The Chapman-Robson estimation procedure remains appropriate with recoveries from marking and tagging (Paulik 1962). However, if marked animals are introduced over a series of years, the way is then opened for a wide range of estimation procedures along with some additional tests of assumptions. An extensive set of models and estimation procedures was developed by Brownie et al. (1978), mainly with reference to applications to bird-banding. A general method of analysis based on numerical solutions of maximum-likelihood estimators was proposed by White (1983), and illustrated on a set of large vertebrate data. The book of Seber (1982) contains the most extensive coverage of methods, but should be supplemented with the recent monograph by LeBreton et al. (1992) which covers recent developments and lists the many computer programs now available for processing data.



One of the more troublesome aspects of use of marking and tagging for estimating survival is that only a relatively small fraction of marked individuals are ever recovered. This opens the door for a variety of biases (cf. Pollack and Raveling 1982) and results in substantial variability in the estimates. A logical approach to the difficulty is then to use telemetry, so that status of individuals is largely known throughout life of the transmitters. Relatively little quantitative work has yet been done on survival rates estimated from telemetry data. A useful reference dealing with circumstances in which survival of an individual is checked at irregular intervals (Bart and Robson 1982) gives results that should be useful in telemetry studies, while Heisey and Fuller (1985) specifically discussed estimation of survival rates by telemetry, as did Pollock et al. (1990).

A problem in using these methods is that they are based on the assumption that survivorship is constant from day to day and among individuals. The results may thus be suitable for relatively short time intervals, but cannot safely be extended to longer periods, such as a year, due to the prospect that daily rates cannot be assumed constant throughout long periods. An alternative is to do the analyses in terms of years, not days. This will, in most cases, be necessary for long-lived animals in any case, due to infrequency of mortalities. Another issue in need of attention is that of censoring, i.e., individuals may be lost to observation when the radios cease to function or by emigration from the study area. Also, in long-lived species, many of the tagged individuals will remain alive at the end of the study period.

### 7.5 Reproductive rate estimation

For those species that reproduce annually, there usually is little serious difficulty in obtaining estimates of reproductive rates. The major sources are observations of pregnancy rate and tallies of young per adult female. Normally only pregnancy rates can be determined on an age-specific basis. In any case, survival rates for the youngest age class used need to be defined in terms of the reproductive rate used, e.g., if pregnancy rates are used then early survival includes mortalities in late-term pregnancy.

Species that do not reproduce annually may pose some special problems in estimating reproductive rates, particularly when direct observation is not feasible. It may then be necessary to use a composite rate, based on different sources of data. Litter size may be directly observed, while sex ratios of young may be available only from those individuals that can be caught and handled (often sex ratio is simply assumed equal at birth). The composite rate might then be computed as:

$$m = \frac{(\text{sex ratio})(\text{mean litter size})}{\text{breeding interval}}$$

Direct measurements of breeding interval are likely to require marking or tagging, and may best be done with radiotelemetry to reduce the prospect of missing a reproductive event. Knight and Eberhardt (1985) discuss problems in estimating this composite rate for grizzly bears.

In some situations it may be feasible to substitute proportion giving birth rather than breeding interval since, in an equilibrium situation, the proportion giving birth will approximately equal the reciprocal of breeding interval. When single births are the rule, if sex ratios are assumed equal, then  $m$  simply equals proportion giving birth. It is, of course, necessary to assume that only fully mature females are involved in the calculations. In reality, individuals usually do not reach full reproductive capability in a single year, so that some corrections for reproductive rates of younger animals may be needed.

## 7.6 Projection models

The major uncertainty in using projection models is whether or not some functional representation of density dependence needs to be incorporated in a given example. Although most ecologists largely accept density dependence as reality, there simply is not enough information available to specify how it may apply in particular circumstances. If regulation is to be considered in a projection, then a specific model has to be used. Two classes of models have been used in actual applications concerning vertebrates. The model used for large vertebrates has been described as a "generalized logistic":

$$r_t = r [1 - (N_t/K)^z] \quad (7.3)$$

where the annual rate of increase ( $r_t$ ) is reduced from a maximal rate ( $r$ ) as the population ( $N_t$ ) increases towards an asymptotic value ( $K$ ). The rate ( $z$ ) controlling approach to the asymptote determines the inflection point:

$$p = (1 + z)^{-1/z} \quad (7.4)$$

When  $z = 1$ , this model reduces to the discrete form of the ordinary logistic growth model, hence the term "generalized logistic". The main practical application thus far has been in calculations performed for the International Whaling Commission.

The second class of models used in practice includes the stock-recruitment models of fisheries research and management. The two main forms are those of Beverton and Holt and of Ricker (Ricker (1975) gave extensive details). The Beverton and Holt curve is essentially based on the ordinary logistic growth curve. As a growth model, Ricker's model can be shown to be essentially equivalent to the Beverton and Holt curve when  $r$  is in the range typical of large vertebrates (Eberhardt 1977c). It is only when annual rates of increase approach those reported for some species of fish that the two curves need to be distinguished.

Probably the only real assurance as to whether a functional model of density dependence needs to be incorporated in a given actual projection comes from experience. There is a slowly increasing body of evidence that the inflection point for large mammals is usually well above the 50 percent level of the ordinary logistic curve (Fowler 1981). If this is generally true, then it may not be necessary to utilize a density dependence function in a projection model unless the population approaches relatively high levels. At present, past experience with the particular population likely has to be the principal source

of guidance on this score. Eberhardt (1987) described growth patterns for 16 populations with a simple exponential curve, but also found it necessary to use a density dependent function at higher levels for several of these populations.

In a number of cases, projection-type models have been used for "back-calculations". Most examples result from the need to compare present population levels with likely pre-exploitation abundance (see, for example, Breiwick, Eberhardt and Braham 1984). It will then be essential to include density dependence in the model, and the inflection point chosen will have an appreciable impact on outcome of the back-calculation. Most such back-calculations have been made to comply with regulations that mandate a given population should not be reduced below its "maximum net productivity" or maximum sustainable yield level (cf. Eberhardt 1977a). However, choosing different inflection points may influence the outcome substantially.

When it comes to actually using a projection model with data, very little work has been done with fitting matrix models to large vertebrate populations. This is largely a consequence of the fact that the necessary data are usually not available. About all that can presently be done is to attempt to estimate the essential parameters for the Leslie matrix at some point in time. If population estimates for a series of years are available, it may then be feasible to attempt to see how well matrix calculations "track" the observed data. If age structure data are also available for a number of years, it should then be possible to attempt to estimate some of the parameters in the matrix by iterative fitting procedures using a chi-square criterion.

In the much simpler case where the projection model is a difference equation, it may then be feasible to estimate parameters by direct fitting procedures (some examples were given by Eberhardt 1987). If it is necessary to use equation (7.3), or some other functional representation of density dependence, then the fitting will become much more complicated.

## 7.7 Some historical features of population analysis

The word "population" derives from the Latin *Populus*, meaning people, while "demography" stems from the Greek *Demos*, also meaning people. These roots indicate clearly the origins of the terminology and methodology now applied to aggregations of all kinds. It is now common practice to use "population" to mean any well-defined collection of objects, both animate and inanimate. There are, however, those who interpret "demography" as meaning only the study of human populations. Because the bulk of the techniques in use in ecology stem directly from early work on human populations, it seems pointless to use a separate term for animal and plant populations. It is obviously bad grammar to use "animal demography".

An excellent review by Cole (1954), under the title "Sketches of general and comparative demography", provides many interesting historical details, and is the basis for much of the present section. Students should also refer to the book by Allee et al. (1949) for additional perspective on origins of ecological population studies. Although over 50 years have elapsed since this book was published, it is still one of the better references, due to its detailed and thorough coverage of many features of animal ecology.

Population enumeration was no doubt practiced well before the census was developed by the Romans, and an elaborate system of population registration was in use in China before Marco Polo's time. Surprisingly enough, not until the 17th century did the "modern" nations begin complete population enumerations. Cole (1954) suggested that "Plato, and probably Solon before him, had a definite concept of an optimum population size and an understanding of factors regulating population size."

An Italian, Botero, in 1588 clearly recognized the limitations placed on population growth by environmental resources. He also preceded Malthus by some two centuries in formulating the concept of potential geometric growth of populations. Skellam (1955) noted that Linnaeus (in 1740) described potential population increase in plants by a geometric growth scheme, thus also preceding the famous 1798 essay by Malthus.

The Romans sold annuities at rates that changed with advancing age, but it was not until 1662 that the basis for an effective life table was developed by John Graunt, and then refined into something approaching modern versions by Huygens in 1669. In the 1750's Buffon enunciated a clear qualitative statement of the principles of the "balance of nature", while a century later Darwin and Wallace produced the ultimate key to evolutionary understanding. In the same period, the forerunners of modern mathematical and statistical development were at work. These included Quetelet, Gompertz, and Verhulst (in the 1820's and 1830's) followed by Galton and the rapid development of biometric methods culminating in the work of Karl Pearson and his associates in the early 20th century. Modern mathematical approaches to demography were pioneered in the early 20th century by Pearl, Lotka, and Volterra.

## 7.8 A classification of methods for estimating abundance

The classification used here rests on a basic dichotomy between situations where plants or animals can be readily and directly counted, and those where this is not feasible. The direct sampling methods can be further subdivided in terms of the sampling units employed in the field. Indirect sampling methods can be conveniently subdivided in terms of whether or not an individual animal is likely to be observed on more than one occasion. Single observations necessarily result when the animal is killed (e.g., catch-effort methods) and are generally expected for most of the index methods. Repeated observations on individuals are necessary for the capture-recapture methods.

The classification is given below in segments, with each unit followed by a brief discussion. References to Chapters or Sections are included, along with a few special literature citations. Additional references are included in the appropriate chapters. The classification is adapted from one given by Eberhardt (1978a). The first section deals with direct counts of individuals.

\*\*\*\*\*  
 Classification                      Applications                      References  
 \*\*\*\*\*

I. DIRECT SAMPLING	Used where direct counts are feasible	Chapter 4
A. Area counts		
1. Discrete sampling units	Parasites on or in hosts, colony counts, artificial substrates, sampling catches of individual vessels, time-area counts	
a. Counts of all individuals or absence		
2. Quadrats		
a. Counts of all individuals	Counts of plants, deer drive counts, corers.	
b. Tally of presence or absence	Used in attempts to reduce sampling effort	
c. Proportion of plot occupied	Used for plants when individuals difficult to distinguish.	
7. Strip transects		
a. Counts of all individuals	Counts of plants, inanimate objects, sessile animals.	Section 5.10
b. Partial counts		
i. Visibility decreasing with distance	Animals that do not flush or are sessile, plants, inanimate objects.	
ii. Intermittently visible	Marine mammals	
B. Counts at fixed points	Counts at dams or weirs, or vantage points along streams or coastlines (usually migratory species).	
C. Line methods		
1. Line intercept	Plant canopies and other sizable objects	Section 5.3
2. Line transect		
a. Animal flushes	Animal censuses	Section 5.5
b. Searching by observer	Inanimate objects, animals that do not flush	Section 5.6

## D. Point methods

- |                     |                             |                    |
|---------------------|-----------------------------|--------------------|
| 1. Point frames     | Plants                      | Greig-Smith (1964) |
| 2. Distance methods |                             |                    |
| a. Radial           | Plants, sessile animals     |                    |
| b. Linear           | An alternative arrangement  |                    |
| ("variable-         | more suitable for use in    |                    |
| area" plot)         | the field.                  | Section 5.4        |
| 7. Bitterlich       | Used to estimate basal area |                    |
| method              | in forestry                 | Section 5.4        |
| ("angle-count")     |                             |                    |

\*\*\*\*\*

An important distinction in "area counts" is whether or not natural groupings can be accurately distinguished. Examples of such natural sampling units include individual plants, beaver colonies, fishing vessels, and the like. When natural sampling units are not available, or cannot be precisely delineated, some sort of artificial sampling unit has to be defined. The commonest example is a sample plot or quadrat. When natural sampling units are available, two factors must be considered. One is whether or not a random sample of such units can be obtained, and the other is whether all of the items of interest on selected units can readily be enumerated. If random sampling of units is feasible, and complete counts of individual items on the units are readily obtained, then standard sampling methods are appropriate. When there are difficulties with either factor, then other techniques need to be used. These can be quite complex, as will be evident from looking through any of the sample survey texts (e.g., Cochran 1977). However, a simple approach that works well in many practical situations is to use a plot sample to estimate the number of units, and then to tally the items of interest on all or a subsample of the natural units falling in the plots (cluster sampling).

In the case of either discrete sampling units or quadrats, various efforts have been made to reduce the labor involved in tallying individual plants and animals by only recording whether there are any individuals present or not ("presence and absence" data). Sometimes this information is all that is wanted, e.g., in determining the proportion of plants or animals infested by parasites. However, when this approach is used as a shortcut for estimating a total count, it usually fails. This is because the usual underlying assumption is that the individual items (e.g., parasites) are randomly distributed to sampling units (hosts). If this is the case, then the binomial distribution (or Poisson approximation) holds, and the proportion of "zero counts" can be used to estimate a total number or density. Almost invariably some kind of clumping or "contagion" (i.e., non-randomness) holds, and the method does not work. It may be possible to assume some kind of non-random distribution (e.g., the negative binomial) and proceed to make an estimate from the frequency of zeros postulated by that distribution. Unfortunately, this involves knowing or estimating one or more additional parameters for the assumed distribution, so that it is almost always better to resort to stratified sampling or ratio estimation.

Some plants do not have readily distinguishable individuals, so that counts are very difficult. In this situation, and when it may not be desirable to attempt to tally all of the individuals present, one may simply resort to measuring or estimating the proportion of the plot covered by vegetation. An

alternative is to measure the biomass present, either by clipping and weighing material on the entire plot, or by subsampling.

Strip transects are essentially long, narrow plots, and thus can be treated by the methods already discussed. They are, however, discussed separately because of the close connections with other transect methods, and in consequence of some special problems. One is that of objects present on the transect strip, but not observed, and another is that a set of sample transects may have quite different lengths, requiring some provisions for adjustments.

Counts at fixed points have mainly been used for migratory species, but not much statistical analysis has been done on the resulting data, or in designing appropriate sampling schemes. Stratification may be the best approach, with strata being times of day, season, etc.

The "line" methods have two major categories. One depends on the interception of some sizable object by a line laid out by the observer. Data may be collected to either determine the proportion of the total area covered by the objects, or the number (density) of objects on the study area. Two different measurements are taken (length of interception, and width of object), and these permit unbiased estimation. The line transect methods depend on measurements of distances from a transect line traversed by the observer to objects of interest. When the "objects" are animals that are observed because they are startled (by the observer's approach; they "flush"), one kind of theory seems appropriate. If, on the other hand, detection depends on the observer's locating the object, a different theoretical approach may be preferred. .

The "point" methods depend on measurements taken at sample points. In one version, the points are projected onto vegetation (e.g. by a set of long thin metal pins, a "point frame") to determine proportions of vegetative cover provided by various species. Several problems exist, including layering of vegetation and inefficiency in sampling, and the method is not very widely used.

The distance methods have several variants, but the best-known and most useful depend on the distance between a randomly selected sampling point and the  $n^{\text{th}}$  nearest object of interest (usually a plant). Although there has been much interest, and variety of theoretical developments, the current picture seems to be one of use for studying pattern, and not for estimating density. The basic method depends on searching outward in a spiral from the sampling point until the  $n^{\text{th}}$  object is located. This can be rather difficult in the field, so an alternative method is worth considering. This is to use an open-ended plot that is extended until the  $n^{\text{th}}$  object is located. The underlying theory approximately that of the conventional plot approach if  $n$  is large enough..

The Bitterlich method is mainly used by foresters, and has an interesting connection to line-intercepts. The basic method depends on whether or not an "angle-gauge" appears to be narrower than the apparent width of a tree-trunk. The remaining methods are based on indirect tallies of various kinds, conveniently split into two sections based on whether or not

individuals need to be observed on more than one occasion. The first segment deals with methods that require only a single observation of individuals.

\*\*\*\*\*

Classification	Applications	References
----------------	--------------	------------

\*\*\*\*\*

II	INDIRECT SAMPLING	Used where direct visual count not feasible	
A.	Single observation of individuals		
1.	Catch-effort methods	Mainly used with harvest data; also electro-shocking	Ricker(1975)
a.	Closed population	Population assumed unaffected by mortality, recruitment, emigration or immigration during sampling.	
i.	Variable effort		
(1)	Leslie method	Regression of catch per unit effort on cumulative catch.	Seber (1982:297)
(2)	Ricker method	Regression of log c.p.u.e. on cumulative effort, catchability coefficient large.	Seber (1982:302),
(3)	DeLury method	Regression of log c.p.u.e. on cumulative catch, catchability coefficient small.	Seber (1982:303)
ii.	Constant effort	Same effort applied in each sampling	Zippin (1956,1958)
b.	Open population	Situations where mortality, recruitment, emigration, immigration are likely to be significant.	
2.	Indices		
a.	Visual	Roadside counts, aerial counts, roadkills, transects (unadjusted), census with dogs	Chapter.9 (Overton and Davis 1969:427)
b.	Capture or harvest	Bag and creel census, drift-samplers nets, trawls, set-lines, traps plankton-pumping, grabs, dredges, electro-fishing, poison.	Ricker (1975)
c.	Signs	Fecal counts, dens, mounds and nests, tracks, beds, roosts, scent posts, muskrat houses, beaver dams and lodges, amount of food consumed.	Chapter 9
d.	Auditory		
i.	Active	Echo-ranging (fish, aquatic invertebrates).	
ii.	Passive	Tallies of calls or other sounds.	

\*\*\*\*\*

The catch-effort methods almost universally depend on data obtained by exploitation of a population. It is thus not surprising that they were largely



developed in fisheries management, and continue to be mainly applied in that field. An important part of the development of fisheries usage is due to W. E. Ricker, whose 1975 book should be consulted for more details. The methods largely utilize simple regressions of catch per unit effort (cpue) on either cumulative catch or cumulative effort. In exploitation, effort normally varies from day to day (or week to week, depending on how records are kept), so the variable effort models are of major importance. Seber (1982) used different names for three main equations, but many authors lump the methods as "Leslie-DeLury models". One situation where effort usually remains constant from day to day is that of "removal trapping", i.e., "snap-trapping".

The catch-effort models are very simple and easy to use when the population can be assumed to be "closed", i.e., affected only by the harvests. When the duration of the period of exploitation is not short, it becomes necessary to deal with losses from other causes (e.g., "natural mortality"), and, in some cases, with additions to the population ("recruitment"). In these situations, the models may become rather complex, and the results may be quite unsatisfactory unless additional information about the population is available. One way to provide such auxiliary information is to introduce tagged animals into the population at various times. Readers faced with this situation are advised to consult Ricker's (1975) book. Surprisingly little use has been made of catch-effort methods on game harvest data, which is unfortunate, considering that such data are quite widely available.

A major source of information about relative levels of populations has received very little quantitative and statistical treatment. This is data that can be expressed as an "index of abundance", or measure of relative abundance. The classification given above amounts to a convenient way to categorize the data by the means by which an animal's presence is observed. The actual analysis of such data depends on some sort of model, on the sampling method used, and on any auxiliary information that may be available.

Some indices can quite readily be converted to direct estimates of population density, given the appropriate conversion data are available. One example is the deer pellet-group count. Other indices may be expressed in terms of population density but are known to be biased. Conceivably these methods might be treated separately as direct estimates of abundance, but they seem most readily dealt with as indices. The best known census methods depend on repeated observations of individuals (the capture-recapture methods) and are usually divided into the simpler applications requiring the assumption of a closed population, and the more complex situations where a population is "open" to losses and gains. We first consider methods appropriate for closed populations.

*****		
Classification	Applications	References
*****		
B. Repeated observations of individuals		
1. Capture-recapture	Mobile and secretive animals	Chapter 8
a. Closed population		
i. Petersen method (Lincoln Index)	Usually only 2 sampling periods. May also be applied with stratification.	Section 8.2
(1) Basic method		
(2) Sampling with replacement	Second sample by visual observation.	
(3) Sequence of removals	Second sample taken as sequence of observations (e.g., tag recovery in commercial fishery).	Seber (1982:125)
(4) Subsampling	Second sample observed on random sample of subareas.	Seber (1982:111)
(5) Inverse sampling	Second sample size (tagged or untagged) fixed in advance.	
ii. Schnabel method	More than 2 sampling periods; tagging continues throughout sampling.	Section 8.3
(1) Basic method		
(2) Mean Petersen method	Petersen estimates from successive pairs of samples averaged; may reduce effects of departures from assumption of closed population.	
(3) Inverse and sequential methods	Fixing number of tagged or untagged to capture in advance.	
(4) Corrections for catchability	Attempts to correct for violation of assumption of equal probabilities of capture.	
(a) Frequency of capture methods	Number not captured estimated by fitting frequency distribution to capture data.	
(b) Marten's model	Assumes catchability changes at constant rate.	Seber (1982:150)
(c) Tanaka's model	Regression of log(prop. marked) on log(cumulative marked)	Seber (1982:145)
(5) Multi-sample single-recapture	Each tag release followed by permanent removals (as in commercial fishery).	Seber 1982:193
*****		

As the name implies, the capture-recapture methods depend on catching an animal, marking and releasing it, and then again capturing it at a later time. When the population under study can be assumed "closed", that is,

not to gain or lose members during the study period, then rather simple estimation methods can be used. Also, the marking method does not have to distinguish between individuals. It only needs to indicate that a given animal has previously been captured. The simplest approach (Petersen method) requires only an initial marking, followed by one recapture period.

In the basic method, it is assumed that a sample of the population is somehow marked, and that a random sample is later captured and examined for marks. This provides an estimate of the proportion marked in the total population, so that it is a simple matter to calculate an estimate of the total population size. It is usually assumed that the members of the second sample are all caught at nearly the same time. However, this isn't necessarily the case. It may be possible just to observe the animals on a number of occasions and to record the fractions marked. This amounts essentially to sampling with replacement, and leads to a somewhat different model. In some situations, the second sample may not be obtained from one recapture operation, but may come from a sequence of removals from the population. Data of this kind may be treated by a regression model.

When large areas are under study, it may be necessary to use subsampling, leading to various complications, for which not enough experience is yet available for definite recommendations on procedures. A final variant on the basic Petersen model depends on fixing, in advance, the number of marked or unmarked animals to be captured on the second occasion. Since this is rather difficult to do in practice, the approach is mainly of theoretical interest.

The Schnabel method was developed to deal with situations where animals are captured and released on more than two occasions, and the unmarked animals are marked as they are caught. As the number of capture sessions increases, the number (or proportion) of marked animals will increase, so that some sort of regression analysis can be used to extrapolate to total population size. It is, however, also possible to calculate Petersen estimates for each pair of successive capture occasions, and then average the resulting estimates. This has some advantages when the assumption of a closed population is doubtful. Various arrangements for fixing numbers to be examined in advance of the samplings have been developed for the Schnabel method, but again are mainly of theoretical interest.

One of the major problems in the main capture-recapture models is that probabilities of capture are assumed to be the same for all individuals at any given time. There is a lot of practical experience to show that this is not usually true, so various attempts to make adjustments or corrections have been proposed, but unfortunately none of these modifications seems to work satisfactorily in all circumstances. Three such models are listed in the above classification.

A final variant of Schnabel-like methods is the situation where a number of releases of marked animals is followed by a single capture period. It is of main interest in connection with commercial fishing investigations. The final section of the classification deals with capture-recapture models applied to open populations.

*****		
Classification	Applications	References
*****		
b. Open populations occur during census period.	Gains and losses to population	
i. Jolly-Seber method	Stochastic model, estimates mortality and recruitment as well as population size.	Section 8.4
ii. Bailey's triple-catch method	Limited to 3 sampling periods, simplest instance of more general theory.	
iii. Fisher-Ford method	Deterministic model ("trellis" arrangement of data).	Cormack (1968:476)
iv. Manly-Parr method	Avoids assumption that all individuals have same survival rate as required in Seber-Jolly method	Seber (1982:282)
v. Regression method	Mainly used for survival estimation	Seber (1982:237)
2. Change-in-ratio method	Uses change in ratio induced by known removals. Principal use with harvests, but much wider potential scope.	
7. Bounded count method	Adjustment to maximum observed count (assumes finite probability that every member of population can be counted in a single census).	
*****		

As soon as it becomes necessary to assume a population "open" to additions and losses during the study period, the necessary models become quite complex. The main method in current favor is due to independent work by Seber and by Jolly. It requires that individual tag-releases be distinguishable, since this information is used to estimate additions and losses to the population over time. The earlier methods are mostly now of historical interest, but the Bailey "triple-catch" method is worth consideration as the simplest instance of the more general theory. The Manly-Parr method provides a way to avoid one assumption required by the Seber-Jolly approach.

Two methods of population estimation that do not fit into the above classification are the change-in-ratio method and the bounded-counts method. More experience is needed with both methods to determine their ultimate value. The change-in-ratio method depends on observing some ratio in a population, such as the sex ratio, before and after a removal that is restricted to one of the two classes making up the ratio (e.g., males). The method is conceptually very versatile, and can potentially provide various estimates other than population size, such as recruitment and survival. It also turns out to encompass a variety of other methods, and is thus worth study as a means for understanding the other methods. A practical drawback is that the method will usually be based on observations taken before and after a season of

exploitation. Groupings and spatial distribution of the population are likely to change meanwhile, making for various sampling problems.

The bounded counts method depends on the assumption that it is possible, although perhaps with low probability, to see every member of a population in a given survey. In practice, the confidence limits appear to be quite large, and the method may not be very useful.